This beautiful insect Sir P. Walker has some reasons for believing is from Caraccas; he is however not sure of this being the true habitat.

The head and antennæ are black; the former is punctured, and has a longitudinal groove between the eyes; the thorax is also black; but on either side is a large somewhat irregular red patch, and in front of this is a small spot of the same colour; a small red spot is also observable on either side of the prosternum, near the base of the legs; the sides of the thorax are produced in the middle into an obtuse angle, and it has a transverse indentation behind. The scutellum is of moderate size, of an elongate triangular form, black, obscurely tinted with green, and slightly concave. The elytra are of a most brilliant glossy green colour, and very finely punctured; on the anterior half are some delicate rugæ. The mesosternum is black; the metasternum red, and darkly tinted on the fore part and sides; the segments of the abdomen are also reddish, but are edged with blackish; the tibiæ, tarsi, coxæ, and basal and apical portions of the femora, are black; the remaining portion of each femur is red.

XLVI. *On the Use of the Antennæ of Insects.* *By* George Newport, *Member of the Royal College of Surgeons, and V. P. of the Entomological Society of London.*

[Read 1st January, 1838.]

Most of the following remarks on the use of the Antennæ were prepared for publication in the summer of 1831, and transmitted at that time to the editor of one of the monthly journals,—the Magazine of Natural History,—but from an accidental circumstance were not published. Since that period some of the views here adduced have been advocated by other naturalists. The author, therefore, does not now present them to the Society as entirely novel, but only as being a summary of facts (many of which fell under his own observation) that tend to indicate the true use of these organs.

There are no parts in an insect which are perhaps less understood, or have given rise to more controversy, than the Antennæ. From their being immediately connected with the head, and largely

supplied with medullary matter from the very brain itself, we should naturally conclude that they must be of almost vital importance to the insect, or that the excision of even a portion would at least deprive the insect of its usual faculties. But this, experiments have amply proved is not the case. Every one who has been in the habit of collecting specimens for his cabinet must have remarked how frequently he has met with such as have had one of the antennæ mutilated, or perhaps have been wholly deprived of it, yet the instincts of the little creatures have not appeared to suffer, nor would their existence, probably, have been shortened in the slightest degree by the loss. Yet are these organs regarded with the utmost solicitude by their possessors, and are immediately withdrawn when they happen accidentally to have come in contact with any substance, which at once proves their great susceptibility of feeling as well as the solicitude of the insect for their preservation. Of what utility then are they to the insect? Are they for the purpose of smelling, touching, or hearing? Upon this question the greatest naturalists are undecided, some contending for one sense, some for another, and all supporting their opinions by experiments and plausible reasoning; nor is this diversity of opinion to be wondered at, when the various structures of the organs themselves and the modes in which they are used by different insects are considered. The only method by which we can arrive at a certain conclusion is by connecting experimental observations on the manner in which the antennæ are used by different insects, with remarks on their anatomical structure, and, comparing these, to observe how far they coincide so as to be universally applicable to the whole class, and to indicate the possession of the sense of smelling, touching, or hearing.

First, in our inquiry as to the probability of their use as organs of smell, we may premise, that in vertebrated animals, from man to the reptile, the organ of this sense is situated in the face or anterior part of the head; it consists of two or more apertures, the interior of which is of the most delicate structure, being furnished with small blood-vessels distributed over the whole surface, and anastomosing in minute glands, which secrete a thick mucus. This mucus is diffused all over the membrane, and the olfactory nerves ramify beneath it. It seems to be that the perfection of the sense depends in a great measure on the magnitude of the organ and its nerves, and the extent of surface acted on and properly supplied with mucus. Thus in the human species it has been often remarked by travellers that many of the savage tribes of Africa are distinguished for a very extraordinary acuteness of smell, and

it has been found by the venerable physiologist Blumenbach * that these are the tribes which have the greatest developement of the organ. It is the same with quadrupeds: the animals which subsist on fetid substances, or which trace their prey from the greatest distance, are those in which the mucous membrane has the greatest extent of surface; and Scarpa asserts that experiments on living birds have convinced him that the sense of smell is strongest in those which have the olfactory nerve the largest. The same is the case with fishes; the shark, which is noted for acuteness of smell, has a nervous trunk under the principal fold of the mucous membrane, and also branches in the lateral folds, from which proceed filaments that penetrate and are regularly distributed through the substance of the membrane. From all this it seems to be clearly inferred, that in articulated animals the organ of smell is to be sought for in the existence of a part analogous in structure to the mucous membrane of the nose in vertebrated.

Now to what extent does the general structure of the antennæ seem fitted to exercise the faculty of smelling? Since in no instance with which I am acquainted are the antennæ found to be lubricated with mucus exposed to the action of the atmosphere, and in only one or two cases are they perforated so as at all to resemble the olfactory organs of other animals, I am inclined to think that the more simple structures, the setaceous and filiform, would be best adapted for the olfactory sense, if indeed it resides in the antennæ.

Among those who believe that these are the olfactory organs is the celebrated Latreille.† He observes that the different species of beetles, *Dermestes*, *Sylphæ*, *Cleri*, and *Tenebriones*, perceive at a very considerable distance the smell of dead bodies and decaying substances, to which they resort to deposit their eggs; that such is the case with many species of *Diptera;* that the common blue flesh-fly, deceived by the odour of a species of *Arum* (the carrion-flower), alights on it, and deposits its eggs; and that all these species are distinguished by a greater developement of the antennæ than those of dissimilar habits. He observes also that many male insects have the antennæ much larger than their females, and this he thinks may be easily explained if we suppose these parts to be the seat of smell. Bonnet appears also to be of a similar opinion.

Huber, in his admirable work on Bees, conjectures that the antennæ are the organs either of touch or smell, but does not state

* Blumenbach's Physiology, by Elliotson. Second edition, 1817, p. 141.

† Samouelle's Entomologist's Compend. 1819, p. 26.

to which opinion he inclines; he suggests however that they may be organized so as to fulfil both functions at once. A late author, Mr. Samouelle (in the work just noticed, p. 26), also believes them to be the organs of smell, and founds his opinion chiefly on the observations of Mr. Marsham concerning the habits of the *Ichneumon manifestator*, and which, it must be acknowledged, seem at first to lead to the conclusion. The account given by Mr. Marsham is, that in June, 1787, he observed one of this species on the top of a post in Kensington Gardens. "It moved along," he says, "with great rapidity, with its antennæ bent in the form of an arch, and, with a strong vibratory motion in them, felt about until it came to a hole made by some insect, into which it thrust them quite up to the head. It remained about a minute in this situation, apparently very busy, and then, drawing its antennæ out, came round to the opposite side of the hole, and then thrust them in again and remained nearly the same time. It next proceeded to one side of the hole, and repeated the same operation there. Having now again withdrawn its antennæ, it turned back, and, dexterously measuring a proper distance, threw back its abdomen over its head and thorax, and projected its long and delicate tube at its tail into the hole. After remaining nearly two minutes in this position, it drew out the tube, turned round, and again applied its antennæ to the hole for nearly the same time as before, and then again inserted its tube. This operation was repeated three times; but Mr. Marsham approaching too near, in order if possible to observe with a glass what was passing in the tube, he frightened the insect entirely away."

"About a week afterwards Mr. Marsham was in Kensington Gardens, and saw several of these ichneumons at work. They appeared to pierce the solid wood with their tubes, which they forced in even to half their length, constantly passing them between the hinder thighs, which they closed in order to keep the tube straight when over-resistance would otherwise have forced them to bend. It appeared truly surprising to see an instrument, apparently weak and slender, able, with the strength of so small an animal, to pierce solid wood, half or three-quarters of an inch deep; but on particular attention it was discovered that all those that appeared to pierce the solid wood, did it through the centre of a small white spot resembling mold or mildew, which, on minute examination, was found to be fine white sand, delicately closing up a hole made by the *Apis maxillosa*, and where no doubt there were young bees deposited."

The insects, it appears, often "thrust their antennæ into holes

and crevices, from which they almost immediately withdrew them, and proceeded in search of others." As the ichneumons deposit their eggs in the larvæ of other insects, Mr. Samouelle suggests it as probable that in some instances they found the holes empty, and proceeded in search of those in which the object was concealed; and at the same time he inquires—since the antennæ of the ichneumon are not near so long as the ovipositor or tube, and consequently could not always have touched the larva in which that instrument afterwards deposited the eggs—whether from the above facts we may not conclude them to be organs of smelling?

It must be acknowledged that these facts go farther in support of the opinion than any previously adduced; but I would inquire whether the same facts would not go equally far in proof that the antennæ are organs of hearing? To this however we shall return hereafter.

In July, 1829, I examined the anatomy of the antenna of a male of one of the larger ichneumons, *I. Atropos*, Step., the species that infests the larva of the privet moth *Sphinx Ligustri*, L. It consists of about fifty-six articulations, all of which, excepting only the second, from the base to the tip, are gradually diminished in size, and perforated all round by very minute holes, those nearest the tip having also a few scattered and very delicate hairs. This is the general structure of the setaceous antennæ of most insects. Upon making a section of the antenna, I observed its interior to be very copiously supplied with a limpid fluid, and that in addition to a delicate nerve in the centre which extended throughout the whole length of the organ, were, one on each side, two silver-coloured tubes, from which a number of other minute tubes were produced at every joint. That these were hollow tracheæ I am certain, having divided them longitudinally, and observed their beautiful silvery appearance within. Their structure in every respect resembled that of other tracheæ.* The exterior or bony part of the antennæ was perforated, as above noticed, by very minute holes, and these seemed to me to communicate with the minute tubes proceeding from the larger vessels, but of this I am not quite certain. There were so many of these that I counted eleven on each side of several of the joints through which the section was made.

* I have since found that these tracheæ are derived from some cruciform branches which originate in the head immediately behind the brain, from the superior transverse tracheæ which arise, one on each side, from the first pair of spiracles, and anastomose in the upper part of the head above the cranial portion of the dorsal vessel. See Phil. Trans. 1836, Par. II., p. 534.

Hence it seems probable that, judging from analogy with other animals, and also from the anatomy of the antennæ, that these are not the organs of smell. But let us now proceed to experiments and further observations.

The carrion beetles, *Sylphæ*, L., and other insects that subsist upon fetid substances, appear to be the kinds most fitted for our purpose, as being those in which a strong sense of smell is clearly evinced, and which at the same time have the antennæ considerably developed. Accordingly to these my attention on the subject has been chiefly directed.

During an entomological excursion I met with a female specimen of *Sylpha obscura*, L., that had by some chance been deprived of one of its antennæ. The insect was on a foot-path by the road side, near some decaying animal substance on which it had just fed, and was moving about apparently with some uncertainty, as, instead of running off as is usual with its congeners after being satisfied with food, it stopped, and moved its head and remaining antenna in every direction, and did not seem to be so much affected by sounds as most of its family usually are. What the object of its motions was, is not apparent, but it is evident that, having just fed and being at the same time in the immediate vicinity of aliment, it could not be searching for that, and it is probable therefore its motions were not influenced by the sense of smell. I next endeavoured to ascertain whether the *Sylphæ* can discover the presence of aliment by means of the antennæ when placed very near to those organs. For this purpose I took a male specimen that had been confined for sixteen hours without food, and, placing it in a glass, attached a small piece of flesh within half an inch of it. The antennæ, as is usual with these insects, continued to be moved about on either side, but with nothing remarkable in their motions, while the head of the insect was a little elevated and carried forwards, as if it perceived the flesh, and the palpi were in rapid vibratory motion. It soon approached very near to the food, and at length touched it three or four times with the antennæ, but each time suddenly withdrew them as if they had fallen unexpectedly on something obnoxious, the palpi during the whole time continuing their motion. The insect at length reached the food, and after having touched it once or twice with the extremities of the palpi, their motion ceased, and it commenced feeding, while the antennæ were occasionally in motion as before. This experiment was repeated many times and with precisely the same result. During the experiment it was sufficiently proved to me that the creature discovered its food by the faculty of smell,

and its immediate contact by that of touching with the palpi and antennæ; but I remarked nothing that could in the least induce me to suppose that the olfactory sense resides in the antennæ, or even in the spiracles of the body, as some have supposed.* If this were the case we might reasonably have expected that the insect would soonest have discovered its food when it lay on one side of it in a line with the spiracles or with one of the antennæ, and not when directly in front. On the contrary, the insect frequently moved in an opposite direction, and seemed to find its food most readily when placed, although at a greater distance, directly in front of it. Hence a question naturally arises, if it be neither in the spiracles nor the antennæ, where does the sense of smelling reside? Analogy teaches us to search for it in the head, as suggested by that excellent and venerable naturalist the Rev. W. Kirby, the father of English entomologists, and where after all, perhaps, it may be found.

Animals inhabiting water have the faculty of smelling equally with those which inhabit the atmosphere. This is proved from the known fact that odoriferous substances, often used by poachers as bait, when thrown into ponds or rivers attract fishes from a great distance, in the same manner as they would attract birds or quadrupeds in the atmospheric air. And here I may notice a striking instance of the existence of this faculty in water-beetles, previously to detailing experiments on them with regard to the use of their antennæ.

Towards the latter part of the summer of 1830 I frequently observed many different species of water insects, particularly *Dytici*, *Notonectæ*, and water *Cimices*, sticking to the sides, and lying beneath the wall of an outhouse that had been recently covered with coal tar, and I was awhile in doubt to know what could have attracted so many of such different species to that particular spot, which was at a considerable distance from their natural haunts, there being neither dike nor pond within nearly a quarter of a mile. It at length occurred to me that they must certainly have been attracted thither by the tar, which, it is well known, emits an odour of carburetted hydrogen gas, and which gas is also abundantly formed in stagnant pools and dikes, the usual habitations of those insects. What tends in a measure to confirm my opinion is, that although at the present time (April, 1831), after an interval of nine months from the date alluded to, the odour of the tar is considerably diminished, the same species are still attracted to the spot, and have not been observed on any

* Cuvier and Lehmann.

other part of the premises. It was one of the tribes of insects thus proved to possess the faculty of smelling to a considerable extent that was chosen as the subject for my experiments on the antennæ of the water-beetles. The individual was a female of *Hydaticus cinereus*. This appeared the more fitted for the purpose because the species has setaceous antennæ, and thus appears to offer a more fair comparison with that of the ichneumon above noticed. I had purposely confined the insect for three days without food in a cup about half filled with water, and, at the expiration of that time, attached a small piece of raw flesh to the end of a wire, and carried it several times along the sides of the insect, particularly near the spiracles, where it was suffered to remain for a short time; the insect however did not appear to perceive it, but during the whole time remained in the water perfectly undisturbed. The flesh was then carried very near to one of the antennæ, but without exciting the slightest motion in that organ, while the insect began to move its palpi very briskly, as if it detected the presence of something, but continued in other respects motionless as before. The flesh was then brought in direct contact with the antennæ, and the insect immediately withdrew them as if annoyed, as in the experiment with the *Sylpha*. It was then carried exactly in front, and at about the distance of an inch; the palpi were instantly in rapid motion, and the creature, darting forward, seized the flesh, and began to devour it most voraciously. The following day the experiment was repeated several times, and with precisely the same result, but on this occasion the antennæ were so repeatedly touched with the flesh, that the annoyed insect kept them at last beneath the sides of the thorax.

Hence I think it must appear that, from there being no alteration in the motions of the insect when the food was held near the sides of its body, the sense of smelling does not reside in the spiracles, nor, for like reasons, in the antennæ; while, from the motion of the palpi and the avidity with which the insect darted upon the food when held in front of it, it seems but fair to conclude that the sense of smelling must certainly reside in the head, as above suggested.

The next experiments were on insects with pectinated antennæ, and these, it will be seen, discover their food by means of the olfactory sense. The specimen chosen for my purpose was a male stag-beetle, *Lucanus Cervus*. It had been confined in a wooden box about fourteen days, entirely without food. Feeling satisfied, from an examination of the parts of the mouth, that

vegetable aliment was its proper food, a piece of wheaten bread, well moistened with water, was placed at about one foot distant from it. The insect had previously to this been remaining at rest, but immediately after began to move its palpi, elevated its head, extended its antennæ, put itself in an attitude for motion, and protruded the delicate laciniæ from its mouth, as if in search of something. The antennæ were then alternately elevated and depressed, and used as if in the act of exploring, touching everything within reach of them, both backward and forward, while the palpi continued their motion, and the laciniæ were repeatedly protruded to their fullest extent. The insect then advanced a few paces, stopped, and continued its motions as before. Being on a table covered with a green woollen cloth, and nearer to the aliment, the object of its search, the insect seemed as if deceived with regard to the substance it was placed on, and after firmly attaching its claws, straightening its limbs, and setting them at angles with its body, which was elevated upon them, it began, with extended mandibles, to attempt tearing the cloth, by fixing their forked extremities into it, and with evident exertion elevated itself to the utmost, as if in the act of tearing or stripping off the bark from the root or branch of a tree, and then, depressing its body as closely to the table as possible, extended the laciniæ as if to sip the fluid it instinctively expected to flow from the supposed wound. Upon not finding this, the palpi were again in rapid motion, and the antennæ used for exploring as before. It then advanced a pace or two, and the nearer it approached the food seemed to repeat its motions with greater effort. In order to discover whether the antennæ were the olfactory organs or were merely used as tactors for exploring, the moistened bread was placed within three-fourths of an inch of the side of the head, and within reach of one of the antennæ, but the creature did not turn aside to obtain it. The bread was then placed at the side of the abdomen, near the spiracles, but no difference in the insect's movements was perceived. It was then placed in front, within reach of the mandibles, and the motions of the insect were then evidently greater than before. These experiments, like the former, were repeated several successive days, and always with the same result.

Hence it appears, in the first place, that the insect was rendered sensible of the presence of vegetable aliment, its proper food, by means of the olfactory sense; that this resides somewhere in the vicinity of the mouth, in the anterior part of the head, and that there are good reasons for believing it does no

reside in the antennæ, or in the spiracles of the body. It must also be remarked that the antennæ of this insect are often used for the purpose of touching or exploring, although previously to flight, upon the occurrence of a loud noise, or when alarmed, they are stretched out to their fullest extent, with their plates widely separated, as if to catch the vibrations of the atmosphere.

On a review of the preceding I think it must be admitted that the antennæ are clearly proved not to be the organs of smell, the only observations at all tending to support their claim to the possession of that sense being those on the ichneumon, to which I must advert hereafter.

It has been supposed by many naturalists that insects are not endowed with so acute a sense of feeling as other animals, though it is evident that the antennæ of at least some species possess very delicate perceptions, since if they be ever so slightly touched the insect withdraws them. This, however, is not the case until they are actually brought into contact, whether it be with the most inoffensive substance or the most noxious poison. The antennæ we find, accordingly, are used as organs of touch in many insects, though not in all.

The experiments of Huber on the queen-bee more directly prove the existence of the sense of touch in the antennæ than any others. These observations are known to every naturalist, but I may perhaps be allowed to notice them here in illustration of the use of these organs. He cut off one of the antennæ and found that very little injury was sustained, but on depriving the insect of both a decided effect was observable. From that moment she traversed the comb rapidly, laid her eggs very irregularly, depositing them indiscriminately in the cells, retired to the most solitary parts of the hive, and for a length of time remained motionless. When followed by some of the workers, and treated with their usual attention, she seemed to be totally unconscious of it, seldom requiring honey from them, and, when such was the case, directing her trunk for it with great uncertainty. Contrary to her natural habits, she seemed eager to escape from the hive by rushing towards the entrance, and desisted from the attempt only after several fruitless exertions.

The individual used on this occasion had been retarded in her fecundation, and in consequence laid only the eggs of males. Huber, afraid that her instinct might have suffered from this cause, deprived another female, whose fecundation had not been retarded, of the antennæ, and introduced her into the hive. Exactly the same symptoms were exhibited in this as in the other

case. And although it is usual for two queens, who are present in the same hive, to fight till one be destroyed, the mutilated queens exhibited no animosity towards each other, neither did the inhabitants of the hive appear to distinguish which was their original female. It would thus appear that, after excision of both antennæ, all marks of distinction were lost.

At another time, Huber divided a swarm into two portions, leaving the queen in one and separating these by a double grated partition, which allowed what was going on among the one to be seen by the other, but prevented the two parties from communicating by means of the antennæ or legs. This was for the purpose of seeing what was the mode of intercourse, and also, what effect was produced upon those who were deprived of their queen. They were soon in great agitation, running violently about, striking each other with the antennæ, and entirely neglecting the business of the hive, until at length they began to construct royal cells and became quiet. Those that had the queen with them remained undisturbed and pursued their usual avocations. One portion of the double grating was then removed, so as to prevent the two parties from mixing, but allowing them to communicate with each other by passing the antennæ through the wires. Immediately the bees were seen to collect upon the grating, pass through their antennæ, and touch with them those of the others. The queen herself came to it, and acted in the same manner. The clamour began to subside immediately, each bee touching with its antennæ those of its neighbour, and in a short time the business of the hive was restored. It was thus proved that bees communicate with each other by means of the sense of touch, and that this resides in the antennæ.

The case is the same with ants, as was abundantly proved by the same author. By means of touching with the antennæ, ants originally bred in the same nest are enabled to recognise each other, although they may have been entirely separated many weeks, or even for three or four months.* When about to form a new colony, they caress, and appear to communicate with each other by touching with the antennæ,† and it is by means of these organs they are enabled to induce the *Aphides* and *Cocci* to give out their sweet juice, or, as it is commonly called, honey-dew, which the ants are exceedingly fond of. Their mode of proceeding, which I have had the pleasure of witnessing, and which is well known to entomologists, is to pat the *Aphis* rather briskly on each side of

* Kirby and Spence, vol. ii. 1st Ed. p. 66. † Id. vol. ii. p. 92.

the body with the extremities of the antennæ until it gives forth its sweets, which the ant sucks up very eagerly, sometimes conveying it to the mouth on the tip of the antennæ. The same mode is pursued by the ants with the *Cocci*, excepting only that with these the strokes of the antennæ are so rapid as to be compared with the thrill of the fingers over the keys of a pianoforte.* Many of the ichneumons, and other tribes of Hymenopterous insects, use their antennæ as tactors. When searching for a hole or crevice in which to deposit its eggs, the insect will feel about on every side within reach with its antennæ, proceed for a short distance, suddenly stop and explore with them, and, having found a place fitted for its purpose, thrust them into it, and often remain for some time as if in the act of examining it. Another family of this order use the antennæ in a still more remarkable manner, as I once had an opportunity of observing. On the 25th of May, 1829, about 300 individuals of (I believe) *Eupelmus puparum*, Steph.,† or a species nearly related to it, were produced from two specimens of pupæ of a *Noctua*. They were confined in a breeding-cage, which was so well secured with gauze sides that no insect of their size could either enter or escape. A few of the insects had come forth the day before, when I remarked what appeared a very singular fact, and on this occasion I had abundant opportunity of confirming my previous observations. In the connexion of the sexes, the males were seen to fix themselves on the thorax of the females, and, before any attempt at union by means of the posterior extremity of the body, to bend their antennæ at right angles, and strike with them those of the female on the inner side, with very quick alternating strokes, which were returned by the antennæ of the females, but with much less rapidity. During the whole time the female continued perfectly quiet, with her wings folded, while those of the male were extended and agitated with the most rapid vibratory motion. This intercourse usually continued from five to ten minutes, and at its

* Kirby and Spence, vol. ii. p. 88.

† I am not quite certain that this was the species, but the following are the descriptions of both sexes of the insect. *Male.—Antennæ* brown, slightly clavate, shorter than body, eleven-jointed: first basal joint yellow, one-third of the length of the whole antennæ; third basal joint very short, joints at the apex scarcely distinguishable. *Body:* head and thorax green gold; eyes black; abdomen brown, with a pale band at the base; legs yellow; wings hyaline.

Female.—Antennæ fuscous at the base, shorter than those of the male; mandibles quadridentate; maxillary palpi long, yellow, four-jointed, labial two or three-jointed. Head, thorax and abdomen bronzed; eyes black, abdomen ovate, sting concealed, wings hyaline. Insect much larger than the male.

conclusion there was only a momentary contact of the anal extremity of the bodies of the individuals at the instant of the male leaving the female, after which the latter immediately took flight, while the male was always busily employed in cleaning his antennæ and limbs. At one time I counted seventeen pairs connected in the same manner. What was the object of this intercourse, if it were not copulation, is very difficult to determine. At all events, it seemed to be of the most reciprocal nature, and the antennæ, so far as I could perceive, were mutually employed.*

In the other orders of insects, as well as in many other Hymenoptera, most of the species with setaceous antennæ use them occasionally as tactors. Those which have them very long and delicate—the *Acridæ*, Kirby—often use them for exploring, in a manner similar to the ichneumons. The large green grass-hopper, *A. viridissima*, when searching for food, will frequently first touch it cautiously with its antennæ, and then examine with its palpi before it begins to eat. When passing from one object to another, it often uses them in the same manner as if exploring the way before it begins to move. That this really is the service the antennæ perform in directing its movements, which are not wholly guided by vision, will appear from its often tumbling from its hold when moving rapidly over bushes or rugged surfaces.

The antennæ are employed in exactly the same manner by another insect of the same genus, *A. grisea*. I once confined several of this species for three or four days without water, of which they require abundance, feeding them during the time upon leaves which were not very succulent. They became emaciated and feeble, and almost ceased chirping. Upon moistening the leaves with water, they immediately began to drink; but first, in order to assure themselves of the presence of the fluid, they touched it three or four times with the antennæ, and afterwards with the palpi. What more directly proved to me the discriminating faculty of the antennæ was, that when the fluid on the leaf was nearly exhausted, the insect felt about with them for the veined or channelled part of the leaf's surface, from which the water might be completely drawn off.

* Mr. Westwood has suggested that the antennæ of these males were probably used to excite the female preparatory to the connubial intercourse. I fully agree with him in this opinion. I have seen the antennæ used in a similar manner, but less actively, by the males of the *Melöe* during coition, and also by those of *Athalia centifoliæ*, in which the actual intercourse of the sexes is almost as momentary as it appears to be in the *Eupelmus* above noticed. The antennæ in these instances must, therefore, be endowed with an exquisite sense of touch.

The *Blattæ* employ their antennæ in a manner similar to the *Aeridæ*, moving them about in different directions, and exploring objects with them. The *Trichoptera*, Stephens, carry the antennæ directed forwards, like the *Ichneumons*, and sometimes use them as tactors. This also is the case with some of the *Coleoptera*. The *Telephoridæ*, when in motion, carry their antennæ directed forwards, vibrating them rapidly, and sometimes, but rarely, touching objects with them. The *Carabi* use theirs in a similar manner, but more frequently as tactors than the *Telephoridæ;* and it seems from our previous experiments* that at least one genus of insects with capitated antennæ (*Lucani*) employ them as tactors, but they cannot be so used excepting only by such as have the organs of considerable length. Whether those with moniliform antennæ, as the *Tenebriones*, *Staphylini*, &c., employ them as tactors, I have not had opportunity of observing; at least the *Staphylini* appear to use them in this way occasionally, but whether the *Tenebrio* does so is much to be questioned, since they appear to be almost always directed forwards and upwards.

It is thus evident that many insects use the antennæ as tactors; and these are mostly such as have them of the filiform or setaceous structure. Yet there are many that have them even of these forms that never use them as organs of touch, although they are of such a length as would enable the insect to do so with the greatest convenience. Among these are many of the *Sphinges* and *Phalænæ*, Lin., as well as some *Papiliones*. There are others that have the antennæ of these forms, but which, on account of their shortness, cannot be used as tactors, for which purpose indeed their diagonal direction, and apparent rigidity and want of muscles for motion, would alone disqualify them. Of this all the *Cicadæ*, *Notonectæ*, *Libellulæ*, *Ephemeræ*, some *Culices*, and many others, are instances. There are also a vast number of other insects in each of the orders, in which, from their very different structure, we cannot regard the antennæ as tactors. In some of these the organs are capitated, and the caput divided into plates. The whole of the Linnæan *Scarabæi* have this form. Now we could hardly suppose that an organ composed of a foot-stalk of joints, and surmounted by a plated knob, could be designed for the sense of *feeling*, and the manner in which these insects retract the antennæ when touched accidentally at once assures us they are not; besides which, in the generality of these insects, they would be too short. When they are so used by some *Coleoptera*, as by the *Lucani*, it appears to be but a secondary faculty, and in such instances the

* Page 237.

foot-stalk of the organ is considerably elongated. That the antennæ can hardly be said to be used as tactors when of the petiolated form, appears from the experiments on the *Sylpha* before noticed. Now nearly the whole of the *Diptera* have the antennæ either too short for the purpose, or of a form entirely unadapted to be used as tactors, while the greater number of a numerous class of animals nearly allied to, but now separated from, insects—although composing the *Aptera* of Linnæus—have no antennæ at all. If the sense of touch, therefore, were the primary use of the organs, one would have thought they would more have resembled each other in structure; at all events would never have been wanting, or so short as not to be applicable to the intended purpose, and it must hence appear that their use in every species that possesses them cannot be simply for the sense of touch.

Now by what means is it that animals are endowed with the faculty of hearing? This, as examination will prove, is purely mechanical. It consists in a means of *feeling the vibrations of the atmosphere*, for which I conceive the structure of the antennæ in every species might entirely adapt them. But it may be objected that we have not proved insects to possess the faculty of hearing, before attempting to point out the particular part in which the sense resides. One proof must suffice,—the sexual call of the *Ptinidæ*,—although many other instances might be adduced from almost every order and genus of insects. Entomologists are aware that a male of this family when in search of the female fixes his anterior legs firmly, and by striking with his head makes a noise like the tapping with one's finger against old partitions, pasteboard, or wainscoting. This call is perceived and returned by the female, often at several yards distance. The male advances and repeats the tapping, which is returned by the female, and this is alternately continued until the two have met. I do not allude to this in proof of the antennæ being the organs of hearing, but only to show that insects, and even those with the simple filiform antennæ, are susceptible of sound the same as the larger animals.

Grass-hoppers and butterflies are as sensible of sound as the *Ptinidæ;* on the occurrence of any loud and sudden noise they immediately erect the antennæ, and, when deprived of them, butterflies are evidently severely affected by the loss. I once plucked off the antennæ close to the head from two or three specimens of *Pontia Napi*, Steph., when they immediately rose in the air to a great height, apparently having no means of directing their flight, and were carried in a line before the wind. I tried some of the *Vanessa Urticæ;* and they, after rising a little, dropped down, as

if stupified and unable to keep on the wing. This was the case with several other species, but when deprived of only one antenna they seemed, like other insects, to experience but little inconvenience.

Now that hearing, as possessed by the larger animals, is purely mechanical, there can be little doubt, since the structure of the parts, exercised during the enjoyment of the faculty, fully demonstrates their mode of use. These consist in general of the ear or external portion, so constructed as to receive within its cavity the vibrations of the atmosphere, which, being collected within a passage, are considerably augmented, and thrown with greater force upon the tympanum, a tense and delicate membrane extended across the bottom of the passage, and from this, by means of other minute parts, the sensation is conveyed to the brain. The importance of this organ—the tympanum—for the perfection of the sense, is fully seen, since in no instance with which I am acquainted in vertebrated animals possessing the faculty is this part wanting, although differently situated in different species, and also from the loss of the faculty resulting from any injury by which the elasticity of the tympanum is destroyed. Upon the form of the external ear also the acuteness of the sense is considerably dependant. Thus in those vertebrated animals which are believed to possess the greatest acuteness of hearing, as the hare, rabbit, bat, &c., it is long and tubulated, affording a larger cavity for the reception of aërial vibrations, and a longer passage before arriving at the tympanum, by which the vibrations become very much increased. An approach to this form of organ is found in the antennæ of a genus of beetles, *Coprides*, Steph., to which, from their habits, we may suppose a greater acuteness of hearing to be necessary. These insects, particularly *Copris molossus*, in which I first remarked it, have the antennæ composed of ten joints, the last three of which form the knob or club with which it is surmounted. Each of these joints, which are long, in the form of leaves, when examined on the under side is found to be concave, and constructed like the ears of the hare or rabbit, and internally is supplied by the nerves which extend through the antennæ from the brain. When the insect is in motion, these plates or auditory organs, if we may be allowed so to call them, are extended as widely as possible, as if to direct the insect in its course; but upon the occurrence of any loud but sudden noise are instantly closed, and the antennæ retracted as if injured by the percussion, while the insect itself stops and assumes the appearance of death. A similar use of the antennæ is made by

another family, *Geotrupidæ*, Fab., which also act in the same manner under like circumstances. In one species of this family, *G. Hercules*, the structure of the caput antennæ is different, and more clearly indicates its real use. It consists of three joints, which, upon being closed together, form an oval-shaped knob. The two exterior of these joints are convex outwardly and concave within, the concavities covered by a tense membrane, so that they somewhat resemble a kettle-drum: the middle joint is flat, and has a membrane extended across both its surfaces. There is a space beneath all the membranes, which may fairly be supposed to be furnished with ramifications of nerves from the large one running through all the joints of the antennæ from the brain.

Here then we have a structure which almost positively indicates that the antennæ are for the function of hearing, since if the lamellæ are not for the perception of sound, they would answer no purpose at all, not being adapted for any other sense; and the antennæ of insects would form a singular exception to the economy and fitness of nature's works, since in no class of animals do we find so great a variety of structure in the same parts, and in none do we find a tense membrane designed for smelling, seeing, or touching, but in every one in which this particular structure is found it exists for the sense of hearing.

These facts, connected with the previous experiments, have convinced me that the antennæ in all insects are the auditory organs, whatever may be their particular structure; and that, however this is varied, it is appropriated to the perception and transmission of sound. We have now to show the means by which the different structures are adapted to this purpose. From the observations above stated I was once much inclined to believe that the seat of hearing, in the antennæ of butterflies and beetles, resides in the caput, but this cannot be the case with moths, ichneumons, &c. The experiments on the ichneumon by Mr. Marsham, as before remarked, are thought to go very far to prove that the antennæ are the olfactory organs, since they could not have touched the object they were examining, being shorter than the ovipositor. But surely they may be equally well suited to the sense of hearing as to that of smelling? Every one must have observed how rapid are the motions of the ichneumon, and how alarmed it is on the occurrence of the slightest noise. Hence, considering the anatomical structure of the antennæ as before described, might not the insect be rendered sensible of the presence of the object of its search—the larva of *Apis maxillosa*—by hearing it breathe, equally well as by smelling? That such was in-

deed the case appears the more probable from observations made both by Scarpa and Fabricius on the anatomy of the setaceous antennæ of the cray-fish, *Astacus fluviatilis*, Leach. Those naturalists found that the tympanum, or seat of hearing, was within the head, at the base of the antennæ, along the hollow cavities of which (and which appear to bear some analogy to the tracheal tubes in the antennæ of the ichneumon) they believed the sounds to be conveyed. Now this opinion is supported by the use which is made of the recently invented instrument, the stethoscope, which is simply a wooden tube, employed by the physician, by interposing it between his ear and the object to be examined, for the purpose of concentrating sounds and enabling him to judge of them with greater precision. Since then the seat of hearing in *Crustacea* is at the base of these organs, we may thence reasonably conclude that it is placed in a like situation in all insects with setaceous and filiform antennæ;* but it may still be objected that there are species with antennæ so formed as to make us doubt whether it be not by other than the means of a tympanum that they are rendered sensible of sound or atmospheric vibrations; and whether the true seat of hearing may not be differently placed in different forms of these organs? Since *elasticity* and *delicate* nervous organization are absolutely necessary qualities of the parts employed in hearing, may not the *elastic ciliæ*, with which many antennæ are covered, be so delicately constructed as to serve for this purpose? If this be not really the case, how are we to explain their use in many insects, particularly in the *Phalænæ*† and some *Muscæ;* and what reason shall we be able to assign for the antennæ differing so much in this respect in the male from the female? By admitting that the ciliæ in these insects perform an office analogous to that of the tympanum in others, the difficulty is overcome, and we see at once a reason why the antennæ of the males in all insects are more developed than in the female, and also why some species have them larger than others.

* The Rev. F. W. Hope has recently stated to me his belief that the organ of hearing is situated in some species at the base of the first or second joint, and this appears highly probable when the occasional large size of these parts is considered. Compare also the remarks of Burmeister, Manual of Entomology, translated, 1836, pp. 295, 296.

† According to Burmeister (Manual of Entomology, translated by W. E. Shuckard Esq., 1836, p. 295), G. R. Trevrianus has described the organ of hearing in *moths* as consisting of a thin drum situated in the forehead at the base of each antenna, but this structure is not found in all insects of other orders. Comparette also appears to have made similar observations in some species.

By means of these, it is probable, the males of many of the foreign *Bombyces*, which are known to fly a vast distance in quest of the females, discover the objects of their search; and our native species, *B. quercus*, *B. potatoria*, &c. find their partners even in the most secluded situations. That they do this by means of the antennæ is highly probable, and that these are employed as the auditory rather than as the olfactory organs is by far more probable. A few objections remain yet to be noticed. The roots of the nerves that go to the antennæ from the brain, being always on the front side of or immediately before those of the eyes, may at first seem to favour the idea of these being for the sense of smell, judging, as we do, from the origin of the olfactory nerves in other animals; but when it is known that in insects there are always other nerves originating from the lower part of the front side of the brain, and more analogous from their situation to the olfactories of the larger animals, this objection vanishes. Lehmann deprived the house-cricket, *Acheta domestica*, Steph., an insect noted for acuteness of hearing, of its antennæ, but the little creature was equally sensible of sounds as before. Now as this insect and its congeners have the antennæ formed almost precisely similar to the cray-fish, is it not probable that the seat of hearing, as in that animal, is placed within the head at the base of the antennæ, whence an excision of these organs would not destroy the faculty of hearing, although, doubtless, it would render it less perfect? Again, it has been remarked that spiders have much acuteness of hearing, yet have no antennæ. The general anatomy of these animals, it is well known, differs greatly from that of insects, and thence it cannot be wondered at that they are differently organized with regard to the auditory organs. May not these be constructed similarly to those of some reptiles that hear very acutely, but which have no external ears, the part answering to the tympanum being on a level, and connected with the common covering of the head, and thence in the spider remain at present undiscovered?

In conclusion, from all that has been observed of the antennæ it seems probable that in all insects these are the auditory organs, and that the means by which they are fitted for the function of hearing are varied in different insects, to adapt them to the perception of sounds according to the habits of the species; that in some species they are endowed also with the sense of touch; that they are of great, although not vital importance to the insect; and that the loss of both of them, more particularly when en-

dowed also with the sense of touch, will clearly explain in every instance the agitation, delirium or stupor of the insect, it being in fact tantamount to a total deprivation of the faculties of hearing, feeling, and, I might almost add, of speaking.

XLVII. *Memoir on the Genus* Holoptilus. *By* J. O. Westwood, *F.L.S. &c.*

[Read 2nd April, 1838.]

The genus *Holoptilus*, belonging to the terrestrial section of the Heteropterous *Hemiptera*, is one of those singular groups, of which examples are to be found in almost every tribe of creatures, which not only attract attention from their peculiar forms, but at the same time baffle the naturalist in his endeavours to arrange them with the existing well-determined families. This difficulty is of a twofold nature, resulting firstly from inaccurate observations on the structure of such groups, and, secondly, from their actual anomalous structure.

The body of these exotic insects is of small size and depressed, and thickly clothed with acute rigid setæ. The head is small, and narrowed behind into a short neck; the eyes are round and very prominent. The ocelli in *H. fuscus* and *Lemur* are very distinct, glittering, and placed on the hind part of the head, at an equal distance from each other and from the lateral margin of the head. They also, as it appears to me upon a careful examination, exist in *H. ursus*, although their existence in that species is denied by Messrs. Saint Fargeau and Serville, who were only acquainted with that species. The rostrum is short and thick, scarcely extending beyond the head, its tip being received in an impression in the front part of the prosternum. It consists of three joints, of which the basal one occupies more than two-thirds of the entire length of the organ, the two apical joints being very short. This is its structure, both in *H. ursus* and *Lemur*, although Saint Fargeau, Serville, and Burmeister, describe the second joint as by far the longest. I cannot discover any short transverse basal articulation, neither can I detect the labrum. The antennæ are long and densely clothed with long rigid setæ, varying in the proportion and apparently also in the number of their joints, as described more in detail below. The thorax is short, divided transversely into two portions, whereof the anterior is the shortest and nar-